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SIZE-ASSORTATIVE PAIRING AND SOCIAL MONOGAMY IN A NEOTROPICAL LIZARD, *ANOLIS LIMIFRONS* (SQUAMATA: POLYCHROTIDAE)

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ABSTRACT. Social monogamy, the formation of stable male-female pairs, is uncommon among reptiles and is particularly rare among squamates, in which only a handful of cases has been reported. Only one case of persistent pair formation has ever been reported in anoles, for *Anolis limifrons,* at a single site in Costa Rica. Detailed studies of *A. limifrons* at other sites, however, have not shown evidence of pair formation. I revisited the site where pairing was originally reported to observe pair behavior in this species and to measure morphological traits of paired and unpaired animals. I confirmed that male-female pairs are commonly encountered in the wild, although a smaller proportion of the animals observed in this study were found in pairs than previously reported. I also found evidence for size-assortative pairing; larger males tended to be found with larger females and smaller males were found with smaller females. I did not find any differences in the morphology of paired and unpaired animals. Although social monogamy has not been widely reported in squamates, I suggest that more examples of this phenomenon will be described as the social behaviors of poorly known species are increasingly subject to study.

KEY WORDS: *Anolis limifrons*; mating system; assortative mating; pair formation; monogamy

Social monogamy, the persistent association between an adult male and an adult female during the breeding season, is relatively common among birds and mammals (Wittenberger and Tilson, 1980), although genetic or mating monogamy is more rare (Petrie and Kempenaers, 1998). Among reptiles however, social monogamy and pair formation are very rare (Uller and Olsson, 2008), and genetic fidelity is almost unknown. Squamates in particular are usually both socially and genetically promiscuous (Bull, 2000; Uller and Olsson, 2008).

There are a few notable exceptions to this generalization (Bull, 2000). The best known case is that of the sleepy lizard, *Tiliqua rugosa*, a long-lived skink native to southern and central Australia (Bull, 2000). This species is active through spring and early summer, when it forages on vegetation, eggs, nestlings, and carrion across a broad home range that can overlap with the home range

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of other individuals of both sexes. Individuals form stable pairs that appear to be socially and genetically monogamous, both within a single breeding season and across multiple breeding seasons (Bull, 2000). Paired animals are often observed in close proximity to each other, and when they are experimentally separated, both males and females actively work to relocate their partners using chemosensory cues (Bull *et al.*, 1993). Pairs of animals can persist over several breeding seasons; one pair was observed together over 10 consecutive years (Bull, 1994; Bull *et al.*, 1998). However, even in this species not all animals are observed exclusively in pairs: 40% of females and 18% of males were found with more than one partner in a season during radio-tracking surveys (Bull *et al.*, 1998). It appears that males that pursue a polygynous strategy do not benefit: females paired with polygamous males were more likely to have multiple-paternity litters, as revealed by microsatellite paternity analyses (Bull *et al.*, 1998). It is unclear whether pair formation is equally beneficial to females and, if so, how.

Australian skinks in the genus *Egernia* have also been shown to form socially monogamous pairs in nature (*E. stokesii*: Gardner *et al.*, 2002; *E. cunninghami*: Stow and Sunnucks, 2004; *E. whitii*: Chapple and Keogh, 2005). In *Egernia saxatilis*, not only do males and females form monogamous pairs, they live in close proximity to their subadult offspring in a situation that mirrors the "nuclear family" found in other vertebrates (O'Connor and Shine, 2003). The Tasmanian snow skink, *Niveoscincus microlepidotus*, also forms pairs that persist, on average, for 29 days during the breeding season (Olsson and Shine, 1998). Aside from skinks, at least two species of Chameleon, *Chamaeleo hoehnelii* and *C. jacksoni*, have also been observed in stable pairs in the field (Toxopeus *et al.*, 1988). In *C. hoehnelii*, pairs persisted for an average of 85 days, and 30–40% of all animals were observed in pairs. In *C. jacksoni*, pairs persisted for an average of 63 days. About half of females were observed in pairs, whereas about a third of males were paired.

Despite these reports of pairing behavior in a handful of species, social monogamy is thought to be extremely rare in squamates. Numerous studies of a wide variety of species support the notion that most squamates are polygamous (reviewed in Stamps, 1983).

Why Monogamy?

Little is known about why some species of lizards associate in pairs while most do not (Bull, 2000). Three non–mutually exclusive hypotheses may account for social monogamy across animal taxa: (1) males remain with females to provide parental care (e.g., food or protection); (2) males guard females because the potential benefit of matings with other females is outweighed by the loss of paternity if other males mate with the focal female; and (3) an individual may remain in the presence of a mate because it benefits directly from their presence (e.g., male may fend off harassment by other males, or both partners may improve the chance of spotting predators; Bull, 2000). Parental care is typically rudimentary or absent in squamates (Gans, 1996); therefore, parental care is unlikely to explain most examples of social monogamy in lizards. A more likely explanation is that either the males, the females, or both directly benefit from pairing with a single partner. One plausible scenario is that monogamy evolves as a consequence of mate guarding in species where it is difficult for males to successfully defend multiple females, such as when females occur at low densities and occupy a broad home range (Emlen and Oring, 1977; Bull, 2000). Alternatively, social monogamy may evolve when

the direct benefits of pairing are especially high, such as when predation risk is substantially reduced by an extra set of eyes.

When monogamy does evolve, the process by which individuals form pairs becomes highly important because an individual's fitness may be closely tied to the quality of its mate. Each individual should therefore strive to pair with the highest quality mates. A common pattern in animals is for the largest males to pair with the largest females and smaller males to pair with smaller females, a pattern known as size-assortative pairing (SAP; Crespi, 1989). SAP can be a product of three processes: mutual mate choice for large body size (e.g., beetles: Harari *et al.*, 1999; spiders: Masumoto, 1999); physical constraints (e.g., beetles: Brown, 1993; fish: Bisazza, 1997); or mate availability—when, for some reason, individuals that are similar in size are more likely to encounter each other and pair by chance (e.g., limpets: Pal *et al.*, 2006). One way that mate availability could lead to a pattern of size assortative mating would be that, on reaching sexual maturity, an animal pairs with the first unpaired, sexually receptive animal they encounter. Older and larger animals are likely to be paired already and smaller animals are not yet sexually mature, so they are most likely to pair with an animal of similar size.

It may be possible to differentiate among these processes based on differences between paired and unpaired animals. For example, if one sex is more abundant than the other, paired animals should be larger than unpaired animals in the more abundant sex if mutual mate choice for body size is operating. In contrast, if physical constraints are responsible for SAP, then the size of unpaired animals should be related to the size distribution of potential mates—large animals may remain unpaired if large mates are rare. Studying SAP can therefore provide insight onto the process of pair formation. In addition, when SAP occurs, it can also have important implications for social behavior, population genetics, and even, potentially, speciation if assortative mating produces a division in the gene pool (Crespi, 1989; Kawecki, 1997; Nagel and Schluter, 1998; Harari *et al.*, 1999; Bessa-Gomes *et al.*, 2003).

Pairing Behavior in *A. limifrons*

A surprising candidate for pair formation and SAP in lizards is a Costa Rican population of *Anolis limifrons*, a slender arboreal lizard that is abundant in a variety of habitats from southern Mexico to Panama (Savage, 2002). This is very unusual behavior for an anole, a genus in which males typically gain access to multiple females by defending a territory and excluding other males (Trivers, 1976; Andrews, 1985; Jenssen and Nunez, 1998; Losos, 2009).

Pair formation in *A. limifrons* was first reported by Talbot (1979), who found that 70% of adults were found in male-female pairs; that is, a single male and a single female were found within 2 m of each other with no other lizards present. Mark-recapture data showed that these pairs persisted for 4–6 months, approximately the adult lifespan for this species. Detailed observations of pair behavior revealed that individuals in these pairs display to each other frequently (Fig. 1) and move in tandem for distances up to 20 m (Talbot, 1979).

Stable pairs have not been observed in other populations of *A. limifrons* despite extensive study; in fact, other populations demonstrate typical resource-defense polygyny (Andrews and Rand, 1983; Andrews and Stamps, 1994). Pair formation has also never been studied in other anoles, though it has been suggested for two species beside *A. limifrons* on the basis of the proximity of

Figure 1. A male *A. limifrons* displays to a female on an adjacent perch. These animals were observed in close proximity and were interacting. No other lizards were observed in the area, suggesting that these animals form a pair.

sleeping males and females (*A. occultus*: Gorman, 1980; *A. cuvieri*: Ríos-Lopez and Puente-Colon, 2007). This study had three objectives: to observe pairs of *A. limifrons* at the site where Talbot collected his data, to determine if such pairs demonstrate size-assortative pairing, and to compare the morphology of paired and unpaired animals.

MATERIALS AND METHODS

Field Data

Field data were collected during a 17-day period from 19 April to 5 May 2007 at La Selva Biological Reserve in the Heredia province of Costa Rica between 7:30am and 5:30pm. Individual *A. limifrons* were spotted by walking slowly along established trails while visually surveying vegetation, a standard method for conducting herpetological surveys (Doan, 2003). When an individual was spotted, two observers positioned themselves approximately 5 m away from the subject. One observer recorded the behavior of the focal animal while the other scanned the area to identify other nearby individuals. If no additional lizards or displays were observed during the first 15 minutes of observation, the lizard was considered "solitary" and was captured. If the initial lizard displayed, or if another lizard was spotted nearby, the observation was extended to 30 minutes. Following the procedure of Talbot (1979), two lizards were considered a pair if they were observed within 2 m of each other, and no other lizards were seen within 5 m during the observation period. In most cases, paired males and females were less than half a meter apart. On some occasions, more than one lizard was observed within 2 m of the initial animal. In all of these cases, a single female was found in the presence of multiple males; multiple females were never found in such a group. It seems likely that these groups represented a pair and one or more intruders but, because it was impossible to determine which male or males were intruding, these cases were excluded from the final analysis (but see supplementary materials to see how the inclusion of these animals would affect the observed pattern). In some cases, more than one individual was identified during an observation, but not all lizards were successfully captured. If a lizard was spotted but not captured, no animals from the observation were included in subsequent analysis.

After 30 minutes of observation, attempts were made to capture all lizards by hand or by noose. Each lizard captured was measured, photographed with the dewlap extended, marked with a unique pattern of colored ink dots on the ventral surface, and released at the site of capture. The data recorded for each individual were sex, snout-vent length (svl, a standard variable for

estimating body size in lizards), forelimb length, hindlimb length, tail length, and the length, depth and width of the head, to the nearest tenth of a millimeter. Males less than 32 mm svl and females less than 35 mm svl were considered juveniles (following Talbot 1979) and were excluded from further analysis (but see supplementary materials to see how inclusion of these animals would affect the analysis). All measurements were taken with digital calipers by the same individual. The surface area of the dewlap was measured for all males in ImageJ (Abramoff *et al.*, 2004) and scaled by reference to a 1-cm grid.

Statistical Analysis

The morphological traits of paired and solitary animals were compared using an analysis of covariance. These traits included svl, fore- and hindlimb length, tail length, head length, width and depth, and dewlap area; body size was included as a covariate in the analysis of all traits except body size. Males and females were treated separately. Because no tests approached significance, no correction for multiple tests was used.

The correlation between body size for members of a pair was calculated using Pearson's correlation coefficient. All statistics were calculated in SPSS.

RESULTS

Among 150 animals observed and captured, 40 individuals were found in male-female pairs; 33 males and 15 females were observed alone; 22 males and 8 females were observed in groups of more than two animals; and 22 males were observed in male-male pairs. Ten males were observed with another animal, but the other individual was not captured and the sex could not be definitely assigned. When animals whose pair status could not be assigned were excluded (e.g., animals in groups, male-male pairs, pairs where one animal was not captured), 57.1% of females and 37.7% of males were observed in pairs (44.9% average for both sexes). Individuals in male-female pairs were often interacting during the time that they were observed, although copulation was never witnessed. Visual displays were performed by both males and females (males displayed in 8/20 observations, whereas females displayed in 2/20). Often one animal, typically the male, followed the other up and down a perch, and from one perch to another (5/20 observations), often moving slowly and frequently stopping until the partner was quite close.

During the course of three observations, a male and female in close proximity were approached by a second male, who the first male proceeded to chase away. While these males were thus distracted, a third male would suddenly appear and approach the female while displaying. In one case, the female approached the third male and watched him display. In the other two cases, the female retreated from the third male. Copulation was never observed during the course of these intrusions.

Male and female body size were positively correlated for paired animals (Fig. 2; $R = 0.50$, $P = 0.039$), and these results were qualitatively similar when smaller animals were included or when animals found in groups with one female and several males were included (see supplementary materials); however, neither body size (Fig. 2), body dimensions, or dewlap area differed between paired and solitary animals (see supplementary materials).

DISCUSSION

Pair formation and social monogamy are rarely observed in reptiles, particularly squamates; yet, during the course of this study,

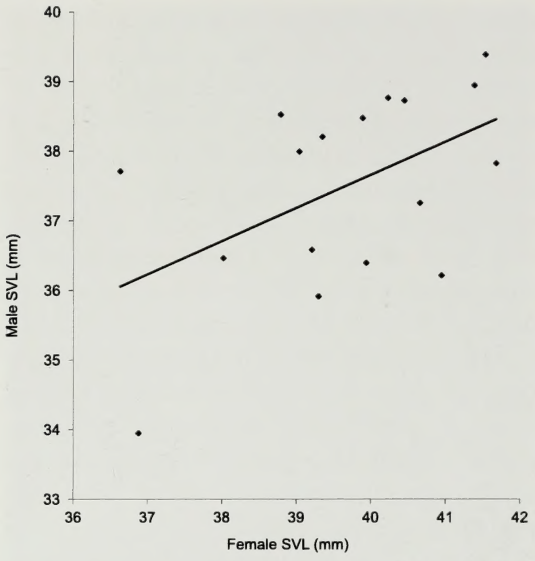

Figure 2. Correlation between male and female body size for paired animals. Each pair is symbolized by a grey diamond.

male-female pairs were observed quite frequently. In most cases, members of a pair were within 50 cm or less of each other and were frequently observed displaying to each other. Pairs also showed coordinated movement, in which one animal (usually the male) followed the female vertically or horizontally through the habitat. These observations, combined with Talbot's (1979) observations of pair persistence over 4–6 months, indicate that these animals are not in association by chance—they are in fact associating in pairs. This social behavior is highly atypical for lizards in general and for anoles in particular, which more typically demonstrate resource-defense polygyny (Losos, 2009). This behavior may also be atypical for *A. limifrons,* which has been shown to defend polygynous territories in other parts of its range. These data also show one of the first reptilian examples of SAP (size-assortative pairing). We found no morphological differences between paired and unpaired animals, suggesting that mutual mate choice is an unlikely explanation for SAP. Two other hypotheses to account for SAP, physical constraints and mate availability, were neither supported nor rejected by these data, but remain a fruitful avenue for future research efforts.

Existence and Prevalence of Pairs

The rates of pairing observed in this study were lower than those observed by Talbot: 45% vs. 70% of all observed individuals, respectively. The lower percentage in this study may have resulted because some paired individuals may have been observed when their partner was not visible, or pairs may have been excluded from analysis due to the presence of a temporary intruder. Unpaired animals might also have been mistaken for paired animals because of temporary proximity to a member of the opposite sex.

It is also possible that the pairing behavior is not typical of *A. limifrons* and occurs occasionally at this location because of unknown environmental or social factors. In other well-studied populations of *A. limifrons*, pairing between males and females has never been reported, despite intensive study (Andrews and Rand, 1983; Andrews and Stamps, 1994). Rather, these populations exhibit a sedentary polygamous mating system based on territory defense, a system typical of anoles. A possible explanation is that *A. limifrons* observed at sites outside La Selva actually belong to a different species, which has diverged in social behavior. Recent morphological work has suggested that *A. limifrons* might actually consist of three or more distinct species (Köhler and Sunyer, 2008). If *A. limifrons* at La Selva comprise a unique lineage, their distinct evolutionary history could have influenced the evolution of their social behavior in a number of ways, via shifts in habitat use, population density, or predation risk, to name a few possibilities.

Another possibility is that *A. limifrons* has a high degree of behavioral plasticity in their mating behavior and that local conditions determine what strategy they pursue. This would be consistent with the polygyny threshold model, which suggests that individual mating decisions may change when the distribution of resources shifts to allow higher densities or stable aggregations of females, or both, that males can monopolize (Altmann *et al.*, 1977). Although data on forest characteristics were not collected as part of this study, it appeared that pairs occur more frequently in primary forest, whereas clusters of animals were found in great abundance in disturbed habitat. This potential pattern could be a productive direction for future studies.

Characteristics of Pairs

Although the data show SAP in *A. limifrons*, I did not find support for the mutual mate choice hypothesis, the physical constraints hypothesis, or the mate availability hypothesis. Paired and unpaired animals did not differ in any of the morphological variables that were considered, including body size; head, limb, and tail dimensions; or dewlap area, suggesting that mate choice is not operating on these traits (see supplementary materials for details). Mutual mate choice may be operating on traits that we did not consider, or a pattern of mate choice in the traits that were examined could have been obscured by the shortcomings of our survey methods or confounding ecological processes that also act on body size, such as differential mortality.

Mating constraints seem unlikely to be responsible for SAM in *A. limifrons* because pairs were observed that were somewhat size-mismatched (and that deviate substantially from the observed correlation), but I cannot rule out this possibility entirely because physical constraints may only be relevant to the most extreme mismatches, and I did not observe all possible size combinations in the population. Captive breeding experiments with highly size-mismatched individuals could be conducted to test this hypothesis explicitly. Likewise, no spatial or temporal discontinuity was observed in the distribution of size classes that would support a mate availability mechanism as an explanation for SAM. However, the spatial distribution of body sizes was not explicitly examined, and the duration of this study was insufficient to uncover temporal patterns of variation in body size. Further studies that explicitly examine the spatial and temporal distribution of body size of paired and unpaired animals may clarify this issue. In short, the process that is responsible for the pattern of SAP in *A. limifrons* remains obscure; uncovering the process of pair formation in this species will require substantial future efforts.

More Questions than Answers

The existence of socially monogamous pairs in *A. limifrons* does not necessarily imply that these pairs are also genetically monogamous. Molecular studies of parentage will be necessary to characterize the genetics of this unusual social behavior. Moreover, we still have little conception of how pairs are formed in the wild or what benefits accrue to pair members. There is a wealth of opportunity for future studies in the field and in the lab on these questions.

The unusual behavior of *A. limifrons* also begs the question: Could social monogamy be more common in lizards than previously thought? The behavior of most species of anole is poorly known from observations in the field; indeed, the behavior of very few lizard species has been studied in the wild. Species that have been overlooked in previous studies are precisely the ones that are

predicted to exhibit social or genetic monogamy; for example species with wide home ranges without established territories or territorial behavior, low densities, and cryptic appearance and habits (Emlen and Oring, 1977). The unusual social behavior of *A. limifrons* described in this study, combined with the fact that it is relatively abundant, easily observed, and geographically widespread, could make this a useful species for future studies of pairing behavior in squamates.

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Note: Supplementary material referenced in this paper is available online at www.mcz.harvard.edu/Publications/.